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Interspecific Relationships Between Egg Size and the Level of Parental Investment per Offspring in Echinoderms

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Abstract. The relationship between the size of an egg and its energy content was analyzed using published data for 47 species of echinoderms. Scaling relationships were evaluated for all species, as well as for subsets of the species, based on mode of development. Regressions were calculated using linear, power function, full allometric, and second-order polynomial models. The full allometric model is preferred because it is relatively simple and the most general. Among these species of echinoderms, larger eggs contain more energy. Egg energy content scales isometrically across a wide range of egg sizes both among and within different modes of development. The only exception is among species with feeding larval development, where there does not seem to be a clear scaling relationship. In most cases, the regressions were statistically significant and explained a very large proportion of the variance in energy content. However, there were wide confidence intervals around the estimated regression parameters. In all cases, the predictive power of the regression was poor, requiring large differences in egg size to yield significantly different predictions of energy content. Consequently, egg size is of limited value for the quantitative prediction of egg energy content and should be used with caution in life-history studies.

Introduction

A major goal of ecological research is to explain the evolution of life histories, *i.e.*, how natural selection modifies reproduction and development to yield the patterns that are observed in nature. Quantitative, theoretical models have been the primary tool used to explore hypotheses on the effects of selection on life-history traits. As a result, theoretical developments became fairly sophisticated and are now considerably ahead of the empirical database. In addition to the emphasis on modeling, the difficulty of obtaining the appropriate data is also responsible for the discrepancy between theory and data. Pianka (1976, p. 782) argued that "A great deal of ingenuity and effort will be required to design and execute research to test this elegant body of theory." Beyond that, Stearns (1977) contended that there might well be fundamental limitations on the kinds of information that ecologists can obtain about life-history evolution.

The relationship between parental investment per offspring and offspring fitness is one of the central tenets of life-history theory that has been particularly difficult to evaluate empirically. Given that the total resources that the parent devotes to reproduction are limited, there should be an inverse relationship between the investment made in each offspring and the number of offspring that can be produced. Further, it has been assumed that as parents allocate more material and energy to each individual offspring, the fitness of the offspring increases because of an increase in the quality of the young (*e.g.*, Smith and Fretwell, 1974). This is a seemingly straightforward and intuitively reasonable assumption. Why has it been so difficult to test empirically?

An important obstacle to the critical evaluation of the relationship between parental investment and offspring fitness is the difficulty in defining parental investment in precise and measurable terms. What exactly are the resources that a parent devotes to its offspring? How can we effectively measure the variation in the level of investment that exists among offspring of a given parent or among the offspring of different parents? Parental care is common

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among animals, and it is extremely difficult to identify components of care that represent quantifiable resources. Time and energy budgets of parents are particularly difficult to measure precisely and even more difficult to quantify in terms of the actual resources that were spent on the offspring.

The problem of parental care can be avoided by studying free-spawning benthic marine organisms. Although some marine organisms do provide protection and care for their young, a very large number are free-spawners, and do not. The latter simply release gametes into the surrounding seawater; fertilization and development occur independently of the parents. In this case, parental investment can reasonably be defined as the material and energy contained in the egg, because that is the only contribution that the mother makes to the young. The paternal contribution consists of the sperm pronucleus and functional centrioles, but this is quantitatively insignificant relative to the contents of the egg.

Given the suitability of free-spawning organisms for measurement and analysis of parental investment, have marine ecologists succeeded in evaluating the relationship between investment and offspring fitness? Unfortunately, no. We have been remarkably unsuccessful in our attempts to acquire data necessary to test and further develop this aspect of life-history theory. This is in spite of a tremendous increase in the interest and research effort in "larval ecology" in recent years.

The failure is due in large part to the fact that marine ecologists have not measured parental investment (as egg energy content) directly; rather they have relied on measurements of egg size as an index of investment. In fact, this is a central assumption of the theory that underlies most of the quantitative models of life-history evolution in marine benthic invertebrates (*e.g.*, Vance, 1973; Christensen and Fenchel, 1979; Pechenik, 1979; Perron and Carrier, 1981; Grant, 1983; Emlet *et al.*, 1987; Strathmann, 1985; Havenhand, 1995; Levitan, 1996; McEdward, 1997). These models attempt to describe the effects of natural selection on egg size, given some reasonable assumptions about the reproductive and developmental correlates of differing parental investment per offspring. "Egg size" is explicitly defined in energetic, rather than geometric, units in these models (*e.g.*, Vance, 1973), to indicate that the quantity of theoretical interest is parental investment per offspring. Unfortunately, use of the term "size" has contributed to the mistaken perception that either geometric size is the primary object of the models or egg dimensions provide a reliable index of energetic size. Nonetheless, given constant reproductive effort, there is an important trade-off between fecundity and energy content per egg. The logical extremes are the production of very many "small" eggs with minimal material or production of very few "large" yolky eggs. The models then predict the direction of evolution of egg size (and related life-history traits) under different environmental conditions.

There are many reasons why it has been convenient, and in fact necessary, to assume that egg size (*i.e.*, egg dimensions) reliably reflects egg energy content. First, it is biologically reasonable that large eggs contain more material than small eggs. Egg sizes span a considerable range in many taxa. For example, in free-spawning asteroid echinoderms (starfish), the egg size range is 2000-fold, from $5–7 \times 10^{-4}$ μl ($\approx$100 μm diameter; *e.g., Asterias vulgaris, Astropecten irregularis, Ophidiaster guildingii, Pentaceraster mammilatus;* Emlet *et al.*, 1987) to about 0.9–1.0 μl (1200 μm diameter; *Perknaster fuscus, Henricia* sp. *(leviuscula?), Pteraster tesselatus*; McClintock and Pearse, 1986; McEdward and Coulter, 1987; McEdward and Chia, 1991). It is clear that very large eggs will contain more energy than very small eggs, regardless of differences in biochemical composition. Given the wide range of egg sizes, obvious questions arise concerning the existence of discernible patterns within this diversity, especially patterns that might reflect taxonomy, adult ecology, biogeography, or mode of development.

Second, for more than 50 years, descriptive and comparative studies have provided much information on what life-history patterns exist, what traits characterize each pattern, and in which taxa and in which environments these patterns occur (reviewed by Levin and Bridges, 1995). There exists a large body of literature showing that egg size is strikingly correlated with important life-history traits such as fecundity, duration of the larval period, larval size, and mode of larval nutrition (see Levin and Bridges, 1995). These studies provide the empirical database from which the theoretical models were developed and within which their assumptions and predictions have been evaluated. Since biologists routinely measure and report egg size, but have not measured egg energy content, the assumption that egg size reflects the level of parental investment is necessary for the integration of life-history theory with the information on reproduction and development of marine invertebrates.

Third, egg sizes (*i.e.*, dimensions) are easily measured, requiring relatively few eggs and no specialized skills or equipment. In contrast, direct measurements of energy content traditionally involve large numbers of eggs and specialized equipment and procedures (*e.g.*, biochemical analyses or bomb calorimetry). However, even when measurements of energy content have been feasible, there remains a serious drawback. Measurement of energy content destroys the egg, making it impossible to know both the level of parental investment and the consequence of that level of investment for the success of the offspring. This is a fundamental limitation on our ability to evaluate the relationship between parental investment and offspring fitness in all groups of organisms. In contrast, measurement of egg size does not harm the egg, but it also does not measure the quantity of theoretical interest. We must, at the very least, assume that

eggs of the same size contain the same amount of energy and materials, if we are to relate parental investment to offspring success using correlations with egg size.

From the reasons given above, it is understandable why egg size has been used as an index of the level of parental investment per offspring. Egg size can be measured simply and nondestructively, it is correlated with many of the life-history features that characterize the patterns we want to explain, and it is reasonable to assume that larger eggs contain more energy and material than small eggs. But, the question remains, is it a valid assumption? Does the measurement of egg dimensions provide a reliable prediction of egg energy content?

Background

Only a few studies have analyzed the relationship between egg size and energy content. Nearly all of the relevant data are from echinoderms, and this is the only group of marine invertebrates for which there is information on egg size, energy content, biochemical composition, and relationships between size and content at different intraspecific levels. In addition, echinoderms exhibit several distinct patterns of development: planktotrophy, pelagic development with feeding larvae; pelagic lecithotrophy, pelagic development with nonfeeding larvae; and brooding, benthic development with nonfeeding offspring that are associated with the parent until they become juveniles.

Strathmann and Vedder (1977) reported that organic matter content was significantly and positively correlated with egg volume among eight species of echinoderms, all with relatively small eggs ($\approx 2 \times 10^{-4}$–36×10^{-4} μl volume, $\approx$80–200 μm diameter) and planktotrophic larval development. Egg content was not proportional to egg volume; rather it was proportional to a fractional power (0.753) of volume. A regression of organic matter concentration (content per unit volume) against egg size had a significant, but negative slope (see Strathmann and Vedder, 1977; fig. 2). They concluded that their results confirmed the assumption that larger eggs contain more organic matter, but they could not explain why smaller eggs had more concentrated organic matter than larger eggs.

Soon after, Turner and Lawrence (1979) examined the biochemical composition of eggs from seven species of echinoderms in order to address a different, but related, question. Are eggs of different sizes and from different species qualitatively alike? They examined species with planktotrophic, pelagic lecithotrophic, and brooding modes of development. Egg sizes ranged from $\approx 2 \times 10^{-4}$–2.4×10^{-1} μl ($\approx$80–750 μm). They reported that both egg size and percentage biochemical composition (protein, lipid, carbohydrate) were variable among species. There was not a relationship between volume and composition. In spite of the variability in size and composition, organic matter content generally increased with increasing egg volume. In addition, they found considerable intraspecific variation in size and composition, especially among individuals from different geographic regions and in different years.

These studies provided empirical support for the assumption that size reflects the organic content of the egg. No one had expected a perfect correspondence between content and size, so the lack of direct proportionality or the variability in composition was of little concern. At the least, there seemed to be a reliable rank correlation between size and energy content that would allow measurements of egg size to be used to infer differences in the level of parental investment among species.

Subsequent research did little to alter the emerging picture of a species trend in egg size and energy content. Lawrence *et al.* (1984) and McClintock and Pearse (1986) reported sizes, biochemical composition (protein, lipid, carbohydrate), and energy content of eggs from nine species of echinoderms. All of the species were from Antarctic or sub-Antarctic regions, had very large eggs ($\approx$1–23 μl volume, $\approx$1200–3500 μm diameter), and all, except for one species, were brooders. McEdward and Carson (1987), McEdward and Coulter (1987), and McEdward and Chia (1991) reported egg size and energy content from nine species of echinoderms with large yolky eggs ($\approx$0.06–1 μl volume, 500–1250 mm diameter) and pelagic lecithotrophic development. Collectively, these species had eggs with very high energy content, and the data confirmed the general trend relating egg size and content.

Several other studies provided new data on egg sizes and energy content or biochemical composition but did not analyze the relationship across species. Jaeckle (1995) reviewed the literature on echinoderm eggs and analyzed the scaling relationship across all species by using linear regression on log-transformed egg volume and log-transformed content (either dry organic weight [DOW] or energy content [*J*]). The striking result from Jaeckle's analysis was that in spite of methodological differences among studies or different measures of egg content (DOW or J), egg content scaled very nearly in proportion to egg volume (scaling exponent 1.06–1.07 $\pm$ 0.05) across the entire range of egg sizes, taxa (classes), and modes of development.

Studies by McEdward and Carson (1987) and McEdward and Coulter (1987) focused on the intraspecific relationship between egg size and energy content. They demonstrated that within species, even within the spawns of individual females, there was considerable variation in size and content. Although statistically significant correlations were found, a very large fraction (61%–88%) of the variation in egg energy content was not explained by the relationship with egg size. Confidence belts were used to evaluate the predictive power of the regression of egg energy content on egg volume (see explanation below). Surprisingly, in most cases, egg size could not be used reliably to predict content.

It is now clear that in general, and on some scales, larger eggs contain more energy and material than small eggs. But the question remains: do egg dimensions provide a reliable and useful prediction of egg energy content? In this paper, we will present an analysis of the relationship between egg volume and egg energy content among species of echinoderms. Our objectives are to identify patterns (scaling relationships) and to evaluate the usefulness of egg size as a predictor of the level of egg provisioning. What is the scaling relationship between egg volume and energy content across species and developmental modes? What is the scaling relationship within developmental modes? What statistical models should be used to describe scaling relationships, and how should those models be evaluated? What is the predictive power of these relationships?

Materials and Methods

Sources of data

To evaluate the relationship between egg size and energy content in echinoderms, we analyzed data obtained from the literature on 47 species, including 22 asteroids, 1 crinoid, 20 echinoids, and 4 holothuroids. Of these, 9 species brood their young, 16 have pelagic nonfeeding development, 21 have planktotrophic larvae, and 1 has larvae that are facultatively planktotrophic. A complete list of the species, with egg volume, egg energy content, class, developmental mode, and literature source, is given in Table 1.

Various authors used different methods to measure egg size and content and reported the results in a variety of units. To facilitate comparison among species from different studies, all of these data have been converted to a standard format and units. Egg volume is reported as microliters (μl) and energy content is given in units of ($J \cdot egg^{-1}$). Volumes were calculated from diameters (d_1, d_2, d_3) using Eq. 1.

$$V = \frac{\pi}{6} d_1 d_2 d_3 \tag{1}$$

In cases where original data on egg size and content for a given species were obtained and reported independently in more than one study, we calculated the arithmetic mean of the published values and reported a single (overall mean) value for the species. Data for egg energy content were incomplete in some studies because the carbohydrate fraction was not reported (*e.g.*, Shilling and Manahan, 1994; George *et al.*, 1997; see Table 1). We calculated the average percentage of carbohydrate (3.54%) for all species in which lipid, protein, and carbohydrate were measured. This average value was used to estimate the carbohydrate fraction for all species in which only protein and lipid had been reported. This calculation made the estimates of total energy more consistent across species and studies; however, because the fraction of carbohydrate is very low, this had a negligible effect on total energy content.

After correcting for missing data on the carbohydrate fraction, we calculated the average "remainder" fraction for all species in which protein, lipid, carbohydrate, and dry organic weight were reported or could be calculated or extracted from figures. The remainder fraction is the difference between the summed biochemical components (protein, lipid, and carbohydrate) and total dry organic (ash-free) weight (DOW). Lawrence *et al.* (1984) and McClintock and Pearse (1986) reported the remainder as an insoluble protein fraction. In other cases (*e.g.*, Turner and Lawrence, 1979; Shilling and Manahan, 1994), the remainder fraction was not reported, but we could calculate it as the difference between DOW and the sum of protein, lipid, and carbohydrate. Turner and Lawrence (1979) did not report specific values for DOW, but, they plotted DOW and summed biochemical fractions in their figure 3. We extracted values from a scanned image of their plot using the Experimental Data Analyst package in Mathematica (version 4; Wolfram Research, Inc.) Using the calculated average % remainder fraction, we then estimated the remainder fraction (R, $\mu g \cdot egg^{-1}$) for those cases where biochemical fractions were reported but DOW was not (George *et al.*, 1997) using Eq. 2, where P, L, C are the protein, lipid, and carbohydrate fractions ($\mu g \cdot egg^{-1}$) and r is the average % (of DOW) remainder fraction. The quotient represents the estimated DOW, including the remainder.

$$R = \frac{\Sigma P, L, C}{1 - r}(r) \tag{2}$$

The remainder fraction has been assumed to be composed of insoluble protein (2.40×10^{-2} J $\cdot$ μg^{-1}) or a uniform mixture of protein, lipid, and carbohydrate (2.70×10^{-2} J $\cdot$ μg^{-1}) by different authors. We calculated total energy content using each of these assumptions, but because the total energy values were so similar, we report only the results from calculation based on the latter assumption. Studies that measured energy content using the dichromate oxidation method were not adjusted for a remainder fraction because all organic material is oxidized and measured in that method. It does not rely on summing separately measured components. No adjustment was made to results from the dichromate oxidation studies compared to results from measurements of individual biochemical fractions. Where both methods were used on the same species (*e.g.*, *Arbacia punctulata*), independently by different authors, the results are remarkably consistent (summed biochemical fractions = 1.416 J $\cdot$ egg^{-1}; summed biochemical fractions = 1.285 J $\cdot$ egg^{-1}; dichromate oxidation = 1.254 J $\cdot$ egg^{-1}). Furthermore, Jaeckle's (1995) analyses explicitly evaluated the scaling relationships as a function of the methods of

Table I

Egg volume (μl), egg energy content (J egg^{-1}), mode of development (P = planktotrophic; L = pelagic lecithotrophic; B = brooded lecithotrophic), and taxonomic class (A = Asteroidea; C = Crinoidea; E = Echinoidea; H = Holothuroidea) for all 47 species of echinoderms

Species	Volume	Energy	Dev	Class	Reference
Arbacia punctulata	0.00022	0.00132*	P	E	Strathmann and Vedder, 1977; Turner and Lawrence, 1979[r]; George, Young, and Fenaux, 1997[cr]
Arbacia lixula	0.00024	0.00281*	P	E	George, Young, and Fenaux, 1997[cr]
Strongylocentrotus purpuratus	0.00027	0.00165	P	E	Strathmann and Vedder, 1977
Paracentrotus lividus	0.00041	0.00284*	P	E	George, Young, and Fenaux, 1997[cr]
Aspidodiadema jacobvi	0.00049	0.00295*	P	E	George, Young, and Fenaux, 1997[cr]
Lytechinus variegatus	0.00061	0.00528*	P	E	Turner and Lawrence, 1979[r]
Echinometra lucunter	0.00063	0.00224*	P	E	George, Young, and Fenaux, 1997[cr]
Stylocidaris lineata	0.00070	0.00317*	P	E	George, Young, and Fenaux, 1997[cr]
Coelopleurus floridanus	0.00080	0.00784*	P	E	George, Young, and Fenaux, 1997[cr]
Dendraster excentricus	0.00090	0.00328	P	E	Strathmann and Vedder, 1977
Asterias forbesi	0.00124	0.00796*	P	A	Turner and Lawrence, 1979[r]
Archaeopneustes histrix	0.00129	0.00654*	P	E	George, Young, and Fenaux, 1997[cr]
Strongylocentrotus franciscanus	0.00144	0.00577	P	E	Strathmann and Vedder, 1977
Pisaster ochraceus	0.00195	0.00783	P	A	Strathmann and Vedder, 1977
Strongylocentrotus droebachiensis	0.00206	0.01218*	P	E	Strathmann and Vedder, 1977; Turner and Lawrence, 1979[r]
Strongylocentrotus pallidus	0.00235	0.00904	P	E	Strathmann and Vedder, 1977
Luidia clathrata	0.00245	0.01986*	P	A	Turner and Lawrence, 1979[r]
Odontaster validus	0.00257	0.01955*	P	A	Shilling and Manahan, 1994[c]
Parastichopus californicus	0.00359	0.00951	P	H	Strathmann and Vedder, 1977
Encope aberrans	0.00359	0.00401	P	E	Herrera, McWeeney, and McEdward, 1996
Encope michelini	0.00510	0.04639*	P	E	George, Young, and Fenaux, 1997[cr]
Florometra serratissima	0.00742	0.04555	L	C	McEdward, Carson, and Chia, 1988
Clypeaster rosaceus	0.01149	0.02060	P/L	E	Emlet, 1986
Cucumaria miniata	0.06398	0.82539	L	H	McEdward and Chia, 1991
Acodontaster hodgsoni	0.08711	0.97715*	L	A	Shilling and Manahan, 1994[c]
Psolus chitinoides	0.09828	1.04957	L	H	McEdward and Chia, 1991
Echinaster sp. 1	0.19912	2.88073*	L	A	Turner and Lawrence, 1979[r]
Echinaster sp. 2	0.23916	4.69026*	L	A	Turner and Lawrence, 1979[r]
Solaster endeca	0.28510	3.55631	L	A	McEdward and Chia, 1991
Echinaster spinulosus	0.31000	3.51600*	L	A	George, Young, and Fenaux, 1997[cr]
Solaster dawsoni	0.37250	4.00467	L	A	McEdward and Chia, 1991
Solaster stimpsoni	0.40600	4.52640	L	A	McEdward and Carson, 1987
Psilaster charcoti	0.44892	2.57138*	L	A	Shilling and Manahan, 1994[c]
Mediaster aequalis	0.45990	5.78792	L	A	McEdward and Chia, 1991
Cucumaria curata	0.52360	4.58365*	B	H	Turner and Rutherford, 1976[r]
Pteraster tesselatus	0.87000	8.26919	L	A	McEdward and Coulter, 1987, McEdward and Chia, 1991
Perknaster fuscus	0.90478	3.1990*	L	A	Shilling and Manahan, 1994[c]
Pteraster militaris	0.90478	10.2000	L	A	McClary and Mladenov, 1990
Henricia leviuscula	1.01000	13.7157	L	A	McEdward and Chia, 1991
Abatus shakeltoni	1.09807	18.1273*	B	E	McClintock and Pearse, 1986[r]
Abatus cordatus	1.25983	16.4600*	B	E	Lawrence, McClintock, and Guille, 1984[r]
Anasterias rupicola	1.34636	18.5340*	B	A	Lawrence, McClintock, and Guille, 1984[r]
Anasterias perrieri	2.80616	39.3162*	B	A	Lawrence, McClintock, and Guille, 1984[r]
Abatus nimrodi	4.00310	45.3448*	B	E	McClintock and Pearse, 1986[r]
Diplasterias meridionalis	11.3713	155.504*	B	A	Lawrence, McClintock, and Guille, 1984[r]
Diplasterias brucei	11.4940	161.297*	B	A	McClintock and Pearse, 1986[r]
Notasterias armata	23.2278	143.019*	B	A	McClintock and Pearse, 1986[r]

* Indicates that values for egg energy content were adjusted as indicated in the Reference column (see text for details).

[c] Values for egg energy content were adjusted for the absence of measured carbohydrate.

[r] Values for egg energy content were adjusted for remainder fractions or by recalculation of the energy value of the remainder fraction.

measurement and found that biochemical fraction data and dichromate data yielded the same scaling relationships.

A complete analysis of the scaling relationships was then conducted for each of the three data sets: the data as originally reported; data adjusted for the absence of the carbohydrate fraction; and data adjusted for carbohydrates and the remainder fraction. The results of these analyses were very similar for all three data sets, so we have reported results only for the "best" or "most fully adjusted" data set in this paper. The fact that adjusting the data did not have a substantial effect on the scaling relationships indicates that the analyses of scaling are robust to details of the data and differences among studies.

Egg diameters and energy contents for the asteroid *Pisaster ochraceus*, the echinoids *Arbacia punctulata*, *Strongylocentrotus droebachiensis*, *S. pallidus*, *S. franciscanus*, *S. purpuratus*, and *Dendraster excentricus*, and the holothuroid *Parastichopus californicus* were measured by Strathmann and Vedder (1977), but were not reported directly. Mean values for each of these species were calculated from the original data and reported by Emlet *et al.* (1987, p. 76) as egg diameter and energy density (=concentration). We calculated egg volume from the reported diameter by assuming that the eggs were spherical (*i.e.*, $d_1 = d_2 = d_3$). We calculated energy content as the product of volume and concentration, using the mean value for energy concentration reported by Emlet *et al.* (1987, p. 76).

Turner and Lawrence (1979, p. 34) reported the organic components of eggs from the asteroids *Asterias forbesi*, *Luidia clathrata*, two species of *Echinaster*, the echinoids *Arbacia punctulata*, *Lytechinus variegatus*, *Strongylocentrotus droebachiensis*, and the holothuroid *Cucumaria curata* (see also Turner and Rutherford, 1976) as lipid, protein, and carbohydrate content ($\mu g \cdot egg^{-1}$). We calculated the energy content of the eggs by summing the energy equivalents of the three organic components and the estimated remainder fraction: lipid = 3.95×10^{-2} J $\cdot \mu g^{-1}$, protein = 2.40×10^{-2} J $\cdot \mu g^{-1}$, carbohydrate = 1.75×10^{-2} J $\cdot \mu g^{-1}$ (Gnaiger, 1983), remainder = 2.70×10^{-2} J $\cdot \mu g^{-1}$ (Jaeckle, 1995). Egg sizes were reported as volumes (Turner and Lawrence, 1979, p. 30) but did not correspond to the egg samples that were analyzed in all cases. Egg diameters were reported by Lawrence *et al.* (1984, p. 253) for the study by Turner and Lawrence (1979), calculated from the appropriate original egg size data. Their calculated diameters represent the diameter of a sphere of equivalent volume; therefore, we calculated egg volumes from the diameters reported by Lawrence *et al.* (1984) using Eq. 1, setting $d_1 = d_2 = d_3$.

Lawrence *et al.* (1984, p. 253) reported diameters and caloric content (cal $\cdot$ egg^{-1}) of eggs from the asteroids *Anasterias perrieri*, *Anasterias rupicola*, and *Diplasterias meridionalis*, and the echinoid *Abatus cordatus*. We converted calories to J using the conversion factor of 4.187 J $\cdot$ cal^{-1} and recalculated the insoluble protein fraction as a remainder fraction. McClintock and Pearse (1986, p. 342) reported egg diameters and energy contents (J $\cdot$ egg^{-1}) from the asteroids *Diplasterias brucei*, *Notasterias armata*, and *Perknaster fuscus*, and the echinoids *Abatus shackletoni* and *Abatus nimrodi*. The energy content values for *Perknaster* were anomalously high and were replaced with the values reported by Shilling and Manahan (1994). We used the average of the two values reported for *Diplasterias brucei* as the mean value for that species. Insoluble protein was recalculated as a remainder fraction. Emlet (1986, p. 186) reported the diameter and organic matter content (μg glucose equivalent $\cdot$ egg^{-1}) from the echinoid *Clypeaster rosaceus*. Egg energy concentration was calculated from organic matter content and size and reported as J $\cdot$ mm^{-3} by Emlet *et al.* (1987, p. 76). We calculated egg volumes from the diameters using Eq. 1, setting $d_1 = d_2 = d_3$, for all of the species in these three studies.

McEdward and Carson (1987, p. 162) reported volume and organic (carbon) content (μg C $\cdot$ egg^{-1}) of eggs from the asteroid *Solaster stimpsoni*. Using the original data, we converted organic content (expressed as glucose equivalents) to energy content (J $\cdot$ egg^{-1}), using a conversion factor of 3.90×10^{-2} J $\cdot \mu g$ C^{-1} based on constants given by Parsons *et al.* (1984). McEdward and Coulter (1987) reported egg volume and egg energy content (J $\cdot$ egg^{-1}) from the asteroid *Pteraster tesselatus*. McEdward *et al.* (1988) reported egg volume and energy content (J $\cdot$ egg^{-1}) from the crinoid *Florometra serratissima*. McEdward and Chia (1991) reported volume and energy content (J $\cdot$ egg^{-1}) for eggs from the asteroids *Solaster endeca*, *S. dawsoni*, *Mediaster aequalis*, *Pteraster tesselatus*, and *Henricia* sp. (*leviuscula?*), and the holothuroids *Cucumaria miniata* and *Psolus chitinoides*.

Herrera *et al.* (1996) reported the egg diameter and energy content (J $\cdot$ egg^{-1}) of the eggs of the echinoid *Encope aberrans*. McClary and Mladenov (1990) measured the egg diameter and energy content (J $\cdot$ egg^{-1}) of the asteroid *Pteraster militaris*. For both species, egg volume was calculated using Eq. 1, by assuming that the eggs were spherical.

Shilling and Manahan (1994) reported egg volume and the protein and lipid content ($\mu g \cdot egg^{-1}$) of the eggs of the asteroids *Odontaster validus*, *Acondontaster hodgsoni*, and *Psilaster charcoti*. Data for *Perknaster fuscus* were not reported directly but were extracted from their figure 2. We calculated estimates for the carbohydrate and remainder fractions. George *et al.* (1997) reported egg volume and biochemical content (protein and lipid, $\mu g \cdot egg^{-1}$) for the eggs of the asteroid *Echinaster spinulosus* and the echinoids *Arbacia lixula*, *Arbacia punctulata*, *Paracentrotus lividus*, *Aspidodidema jacobyi*, *Echinometra lucunter*, *Stylocidaris lineata*, *Coelopleurus floridanus*, *Archaeopneustes histrix*,

and *Encope michelini*. We calculated energy content from the measured energy equivalents (Gnaiger, 1983) for the lipid and protein fractions and the estimated carbohydrate and remainder fractions.

Scaling relationships

Any attempt to describe the scaling of egg energy content *versus* egg size involves a search for a pattern in the data. A scaling relationship is a trend whereby the response variable (energy content) changes in some predictable way as a function of the explanatory variable (egg volume). Two factors influence the description of scaling relationships. The first important factor is the relationship between the variables of interest. This determines the underlying pattern (*i.e.*, the existence and nature of a trend) and accounts for the variance in the variables that is independent of the pattern. The second important factor is the statistical model that is used to characterize the pattern. What is sought is a simple model for which there is a good fit with the data. This involves two steps: selecting the model and then evaluating the fit. The choice of the statistical model imposes on the data the investigator's assumptions about the basic nature of the pattern. Statistical models are selected on the basis of multiple considerations: patterns that are evident when data are visualized graphically, *a priori* assumptions about pattern inferred from the biology of the system, goodness of fit to the data when several competing models are compared, simplicity (biological interpretation) of the model, and ease of calculation. Often, especially with messy biological data, there is no single unambiguously best model. There will generally be a trade-off between simplicity (understandable, but possibly a poor fit) and complexity (nearly perfect fit, but uninterpretable). Very complex models (*e.g.*, higher order polynomials) defeat the purpose of the exercise by describing the data exactly without capturing any aspect of a pattern.

Statistical models

We evaluated four regression models in our analysis of scaling relationships in echinoderm eggs: (1) linear regression; (2) power function regression; (3) full allometric regression; and (4) polynomial (second-order) regression (Table 2). All of the models were fitted by the least-squares criterion as model I regressions (egg size assumed to be measured without error). Although egg size is not measured without error and reduced major axis (model II) regressions would be appropriate, only model I regressions permit calculation of prediction intervals.

Properties of various linear and nonlinear regression models have been examined in detail by Albrecht *et al.* (1993). The linear model has the advantage of simplicity and ease of calculation; it is also biologically reasonable; that is, energy is packaged into eggs in direct proportion to egg volume. The power function model is the traditional form of the allometric equation (Huxley, 1932). It is often approximated using a linear model on log-transformed data. A log-log model $\ln(Y) = \ln(b) + k \ln(X)$ is algebraically equivalent to the power function, but logarithmic transformation of the variables changes the distribution of the data and therefore influences the fitting of the model and the estimation of the regression parameters. An advantage of the log-log regression is that the model is recast in linear form and therefore can be readily calculated. However, with modern software, direct methods of fitting nonlinear models are widely available. Since logarithmic versions of the full allometric and the polynomial models are not possible, the power function was fit directly on untransformed data for consistency with the other models. The three nonlinear models were used to cover the situation in which egg energy scales allometrically (*i.e.*, not in direct proportion) with egg volume. There are many examples of such scaling in biology, and it is easy to imagine reasons why it might apply to egg provisioning, such as changes in biochemical composition with size. The full allometric model, like the power function, can capture nonproportional scaling relationships, but has the advantage of not being constrained to pass through the origin. It is therefore a more general model. The second-order polynomial model captures nonlinearity differently from the power function and allometric model. Whereas the latter models describe nonlinear, continuously increasing or decreasing trends (but not both), a second-order polynomial model is the simplest model that allows for an intermediate maximum or minimum in the response variable. Higher order polynomials can provide exceptionally good fits to virtually any relationship between two variables, including data generated randomly. However, the model parameters do not have any clear biological interpretation.

Table 2

Regression models used in analysis of egg size and energy scaling relationships

Model	Regression equation
Linear	$Y = a + bX$
Power	$Y = bX^k$
Allometric	$Y = a + bX^k$
Polynomial	$Y = a + bX + cX^2$

Analysis of fit

Two criteria were used to evaluate the fit between the models and the data. The first is the proportion of the variance in egg energy content that is explained by its relationship with egg volume. This is calculated as the quotient of the regression sum of squares over the total sum

of squares (r^2 in linear regression and an analogous measure in nonlinear regression; hereafter referred to as fit). The second criteria are the confidence intervals around the estimated regression parameters. All regression calculations were carried out using Mathematica (version 4; Wolfram Research, Inc.) by means of the Regress (LinearRegression) or the NonlinearRegress (NonlinearFit) function in the Statistics standard add-on package. Regression analyses provided parameters of the best-fit model, 95% confidence intervals around the fitted parameters, and the regression ANOVA.

Identification of influential data

Influential data are those values that exert much greater than average influence on the estimation of the regression parameters. The existence of such data can be problematic because then the best-fit regression is based on a small, possibly atypical, subset of the data, and does not reflect any overall trend. Whether such data are outliers that reduce our ability to detect and describe pattern or are particularly information-rich data essential to the detection and description of pattern is a biological, not a statistical, question. We used a regression diagnostic called the Hat Diagonal to identify strongly influential data (Belsley *et al.*, 1980). Once identified, strongly influential data were eliminated from the data set, and the regressions were recalculated to evaluate the effect of these data on the estimation of the scaling relationship and model fit.

Evaluation of predictive power

After quantifying the scaling relationship between egg volume and energy content, we evaluated the statistical significance of that relationship. In addition, we evaluated the predictive power of the relationship, using the approach described by McEdward and Carson (1987). If a regression is statistically significant, then some of the variance in egg energy content is explained by its relationship with egg volume. In that case, it is possible to measure the size of an additional egg and predict its content. Unless the regression explains all of the variance in content, there will be some scatter around the regression line and some error associated with the calculated prediction of content. That error can be estimated by calculating the confidence interval around the predicted value (Neter *et al.*, 1990, pp: 81–84) (Eq. 3).

$$\hat{Y}_h \pm \sqrt{\mathrm{MSE}\left[1 + \frac{1}{n} + \frac{(X_h - \bar{X})^2}{\sum (X_i - \bar{X})^2}\right]} \cdot t_{(1-\alpha)/(2,n-2)} \quad (3)$$

Where $\hat{Y}_h$ represents the $1 - \alpha$ confidence limits for the prediction generated from the new measurement of the explanatory variable (X_h). MSE is the residual mean square from the regression ANOVA, and t is the Student's t statistic with $n - 2$ degrees of freedom.

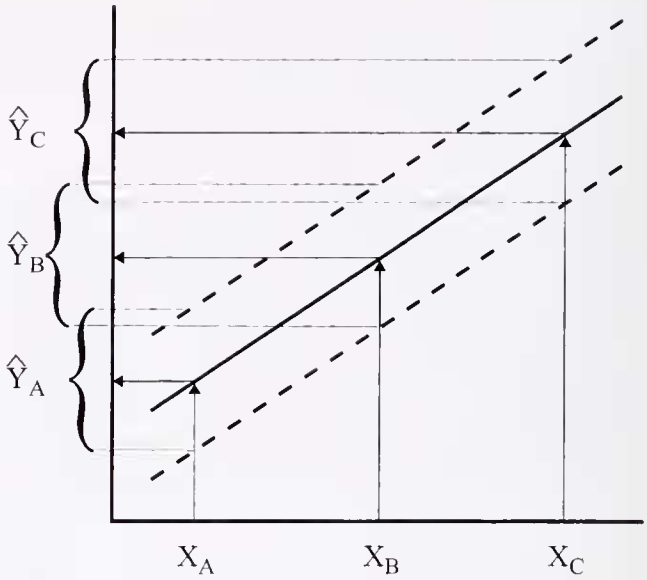

Figure 1. Evaluation of predictive power of a regression using overlap of 95% confidence intervals. Bold, solid diagonal line = least squares regression; bold, dashed diagonal lines = 95% confidence belts for regression. X_A, X_B, X_C = additional measurements of egg size for which predicted energy contents ($\hat{Y}_A$, $\hat{Y}_B$, $\hat{Y}_C$) are calculated using the regression equation (solid vertical and horizontal lines). The 95% confidence intervals for predicted energy contents are obtained from the 95% confidence belts around the regression (dashed horizontal lines). Overlap of the 95% confidence intervals indicates that two predicted egg energy contents are not significantly different. In this example, $\hat{Y}_A$ and $\hat{Y}_C$ are significantly different ($\hat{Y}_A + \mathrm{CI} < \hat{Y}_C - CI$), but neither is significantly different from $\hat{Y}_B$.

To evaluate the predictive power of a regression, we asked: what is the minimum difference in egg size that yields significantly different predictions of egg content? Two predictions of egg energy content were considered to be significantly different (*i.e.*, statistically distinguishable) only if the confidence intervals around them did not overlap (Fig. 1). Starting at the midpoint of the observed range of egg volumes, predictions were calculated for pairs of egg sizes, each pair progressively farther apart, until the confidence intervals around the two predictions did not overlap, or until the entire range of egg sizes had been evaluated. The resolution of this analysis was 0.1% of the observed egg volume range.

The 95% confidence belts around the regression represent the confidence intervals around the predicted egg energy content for all values of the explanatory variable and are needed for our evaluation of predictive power. Both the linear and nonlinear regression analyses generated a table of the single-prediction confidence limits for the actual egg volumes in the data set. From these, we generated equations for the upper and lower confidence belts by fitting the same regression model to the upper and lower (respectively) values of the prediction confidence limits. Given confidence belt equations, it was possible to calculate the confidence limits around predicted egg energy content for any egg

volume between the minimum and maximum observed values for linear and allometric regression models.

The predictive power of a regression depends on the width of the confidence belts around the regression and the slope of the regression. Narrow confidence belts result in greater predictive power because nonoverlapping predictions occur with smaller differences in egg volume (Fig. 1). Likewise, steeper slopes yield greater predictive power because the absolute difference between predicted values is greater for a given difference in egg size than with a regression that has a shallow slope. Hence, predictive power does not have a simple relationship with other regression statistics, such as the fit (proportion of variance in the egg energy that is explained by egg size).

This approach was not feasible with the power function regression model. The reason for this is that the power function regression must pass through the origin, which influences the way that predictive power is estimated. Likewise, the estimation of predictive power with the polynomial model can be misleading because of strong curvature in the regressions (*e.g.*, Fig. 2D). The problem with using overlap of confidence belts with strongly nonlinear relationships is that as the slope of the relationship changes, the overlap of confidence belts changes, and therefore the predictive power changes across the range of egg sizes. Evaluations of predictive power would be valid only over small regions of the egg size range. Rather than report what would seem to be anomalous values for predictions by the power and polynomial functions, we report predictive values only for the linear and full allometric models.

Comparison of means

ANOVAs and Student-Newman-Kuels multiple range tests were used to evaluate differences among taxonomic classes or among developmental modes in mean egg volume or mean egg energy content. All tests were conducted at the 5% significance level.

Results

Brooders make eggs (6.348 μl) that are significantly larger than the eggs of species with planktotrophic (0.0016 μl) or pelagic lecithotrophic development (0.417 μl). Brooders also provision eggs with significantly more energy (66.910 J) than do planktotrophs (0.0087 J) or pelagic lecithotrophs (4.363 J). However, there are no significant differences among the taxonomic classes (excluding Crinoidea with only a single species) in egg size ($P = 0.165$) or energy content ($P = 0.124$).

Scaling relationships for all species

Among these 47 species of echinoderms, both egg size and energy content vary across five orders of magnitude.

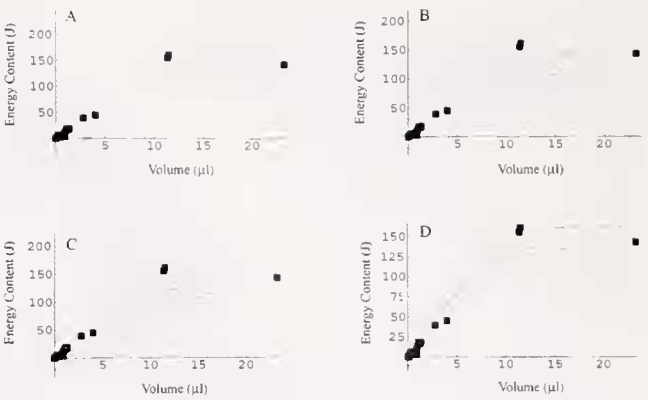

Figure 2. Plots of egg volume and energy content for all 47 species of echinoderms. Panels show different regression models fit to the data and the 95% confidence belts around the regression line. A, linear regression; B, power function; C, full allometric model; D, polynomial model.

There is a strong trend for larger eggs to contain more energy (Fig. 2A). The linear model indicates that the intercept is not significantly different from zero and that egg energy (J) is approximately 8.6-fold greater than the egg volume (μl) (see Table 3 for parameter estimates and regression statistics for all models). The linear regression explains most of the variation in egg content (fit = 84%), but eggs must differ by more than 8 μl in volume ($\approx$35% of the egg size range) to allow the confident prediction that they contain different amounts of energy. This does not provide a useful means of predicting content from measurements of volume. The power function (Fig. 2B) yields a better fit to the data than the linear model, explaining 91% of the variance in egg energy content. The exponent of the power function (0.70) indicates that egg energy content scales with negative allometry relative to egg volume. This means that energy content does not change in proportion to egg volume and that a linear model is inappropriate for

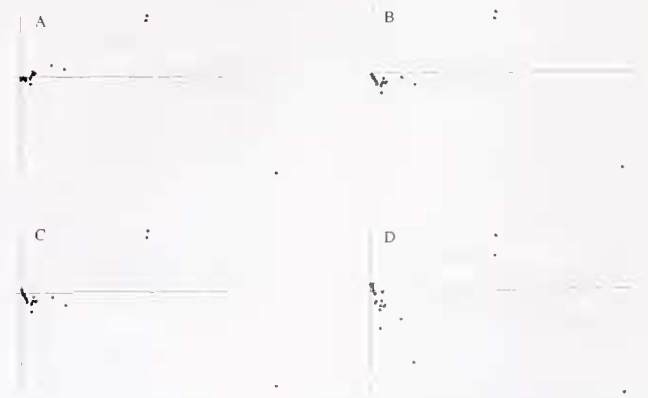

Figure 3. Standardized residual plots for all 47 species of echinoderms. Panels show residuals for different regression models fit to the data. A, linear regression; B, power function; C, full allometric model; D, polynomial model.

Table 3

Regression parameters for all 47 species of echinoderms

Model	a	b	c	k	Fit	ΔX predict Y
Linear	2.607	8.610	—	—	0.838	8.11 μl
	[−2.179–7.393]	[7.474–9.746]				[35%]
Power	—	20.381	—	0.702	0.907	—
		[14.331–26.432]		[0.592–0.812]		
Allometric	−3.141	23.128	—	0.666	0.911	8.36 μl
	[−8.194–1.912]	[14.925–31.331]		[0.543–0.789]		[36%]
Polynomial	−2.201	19.478	−0.561	—	0.984	—
	[−3.922–−0.481]	[18.229–20.727]	[−0.622–−0.500]			

Regression parameters are illustrated for each model in Table 2. Fit is the proportion of the total variance in egg energy content that is explained by the regression against egg volume. ΔX predict Y gives the minimum difference in egg volume needed to yield significantly different predictions of egg energy content.

these data. The full allometric model (Fig. 2C) yields a negligibly better fit than the power function, with nearly the same parameter values. The allometric model has weak predictive power: the minimum difference in egg size necessary to yield significantly different predictions is more than 8 μl. The polynomial regression provides the best fit to the data among the four models tested, with a fit of 98%. It shows that the data are strongly curvilinear (Fig. 2D).

Do any of these models fit well enough to justify concluding that we have described the pattern of scaling between egg size and content? In one sense, yes, using all of the data with fairly simple, general models that were explicitly chosen beforehand yields an objective analysis. Besides, the fit in terms of the explained variance is quite good for all models tested (84%–98%). However, the confidence intervals for the regression parameters are broad in all cases, and this cautions against putting too much confidence in the described scaling relationship. Can the fit of any of the models be improved substantially? Examination of the data (Fig. 2), the standardized residuals (Fig. 3), and especially the Hat Diagonals shows that there is one point which strongly influences the estimated regression parameters. On the basis of this finding, the asteroid *Notasterias armata* was removed from the data set, and the regressions were recalculated.

The most striking result of removing this species is that the relationship between egg size and energy content becomes linear (Fig. 4). With the modified data set, the fits (% variance explained) are exceptionally high (99%), the confidence intervals for all of the regression parameters are quite narrow, and the four models generate very similar parameter values (*e.g.*, the intercept is zero; the slope is in the low teens; and the allometric exponent is only slightly greater than one, indicating nearly proportional or isometric scaling of energy content with volume) (Table 4). In addition, the standardized residuals are more evenly distributed (Fig. 5), and the 95% confidence belts are much narrower. This suggests that *Notasterias armata* is an anomalous

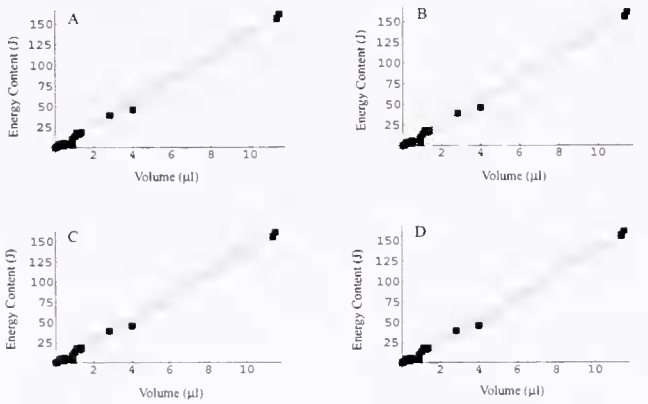

Figure 4. Plots of egg volume and energy content for 46 species of echinoderms, excluding *Notasterias armata*. Panels show different regression models fit to the data and the 95% confidence belts around the regression line. A, linear regression; B, power function; C, full allometric model; D, polynomial model.

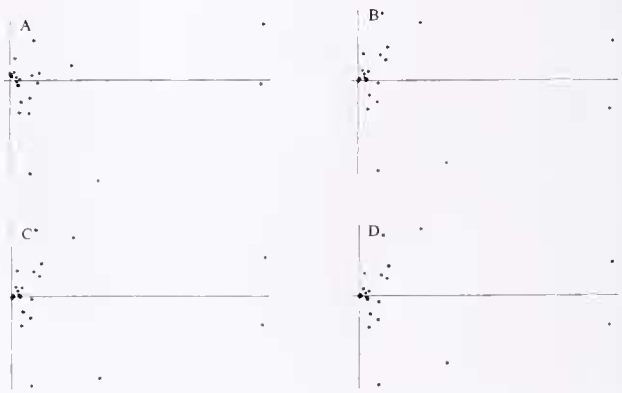

Figure 5. Standardized residual plots for 46 species of echinoderms, excluding *Notasterias armata*. Panels show residuals for different regression models fit to the data. A, linear regression; B, power function; C, full allometric model; D, polynomial model.

Table 4

Regression parameters for 46 species of echinoderms, excluding Notasterias armata

Model	*a*	*b*	*c*	*k*	Fit	ΔX predict Y
Linear	−0.640	13.755	—	—	0.995	0.75 μl
	[−1.360–0.080]	[13.470–14.039]				[7%]
Power	—	11.582	—	1.073	0.997	—
		[10.594–12.570]		[1.036–1.109]		
Allometric	0.094	11.494	—	1.076	0.997	0.69 μl
	[−0.646–0.833]	[10.283–12.705]		[1.032–1.119]		[6%]
Polynomial	−0.038	11.721	0.186	—	0.997	—
	[−0.728–0.652]	[10.673–12.769]	[0.093–0.280]			

Regression parameters are illustrated for each model in Table 2. Fit is the proportion of the total variance in egg energy content that is explained by the regression against egg volume. ΔX predict Y gives the minimum difference in egg volume needed to yield significantly different predictions of egg energy content.

species, in terms of egg size, energy content, or both. All subsequent analyses were conducted excluding this species. The biological basis of the anomalous egg characteristics is not known (see below).

How good is the predictive power of these regressions? Both the linear and the allometric models indicate that significantly different predictions of content require differences in egg volume of 0.69–0.75 μl, which comprise only about 6%–7% of the egg size range. This is substantially less than in the previous analyses, but just how useful is it? Given that the 35 species with the smallest eggs all lie within a range of volumes that spans only 0.52 μl, then it is clear that we are only able to conclude with confidence that very large eggs of species with lecithotrophic larval development (benthic brooding or pelagic) contain more energy than very small eggs of species with planktotrophic (feeding) larval development. These regressions, even given extremely good fit with the data, have poor predictive power.

Scaling relationships within developmental patterns

Is the predictive power of the relationship improved by restricting the analysis to just those species with particular modes of development? In general, egg size and content of planktotrophic and lecithotrophic species are very different (Fig. 2). All species with planktotrophic larval development produce eggs that contain less energy ($\leq 4.64 \times 10^{-2}$ J · egg^{-1}) than eggs from all species with pelagic or benthic (brooded) lecithotrophic development ($\geq 82.5 \times 10^{-2}$ J · egg^{-1}), except for the crinoid *Florometra serratissima* (4.55×10^{-2} J · egg^{-1}) (Table 1). There is overlap in size or content among a few species that represent the extremes within planktotrophy and lecithotrophy. The echinoid *Clypeaster rosaceus* has larvae that are lecithotrophic, in that they do not require exogenous food for larval development and metamorphosis (Emlet, 1986). However, unlike all other lecithotrophic larvae, they have functional feeding structures and can acquire and utilize exogenous, particulate food. This species, being a facultative feeder, has a mixture of traits characteristic of planktotrophic and nonfeeding lecithotrophic larvae. It has a larger egg (1.15×10^{-2} μl) than any obligately planktotrophic species and, with only a single exception, it has greater egg energy (2.06×10^{-2} J · egg^{-1}) than any obligate planktotroph. Only the echinoid *Encope michelini* (4.64×10^{-2} J · egg^{-1}) has greater egg energy than *C. rosaceus*. *Encope michelini* is an obligate planktotroph, but it can complete most of larval development using endogenous reserves and has only a minimal need for exogenous food (Eckert, 1995).

Clypeaster rosaceus produces eggs that are larger than one of the pelagic lecithotrophs, the crinoid *Florometra serratissima*. The eggs of *Florometra* are unusually small (7.42×10^{-3} μl, 4.55×10^{-2} J · egg^{-1}) for nonfeeding lecithotrophs, containing 8.6-fold less volume and 18.1-fold less energy than the next largest egg (*Cucumaria miniata*, 6.40×10^{-2} μl, 8.25×10^{-1} J · egg^{-1}). If *Clypeaster* and *Florometra* are discounted, then the distinction between the eggs of planktotrophs and lecithotrophs is very striking: there is an 12.5-fold difference in egg volume and an 17.8-fold difference in energy content between the largest egg from planktotrophic species (*Encope michelini*) compared to the smallest egg found among lecithotrophs (*Cucumaria miniata*) (Table 1). This difference in egg characteristics is consistent with the nutritional strategies of planktotrophy and lecithotrophy. Obligately planktotrophic larvae must supplement the material provided in the egg by feeding on planktonic particles. Nonfeeding lecithotrophs cannot capture or ingest particles and must rely on nutritional reserves provided in the egg by the parent, possibly supplemented by uptake of dissolved organic matter from the surrounding seawater. The eggs of nearly all brooders are larger and contain more energy than the eggs of pelagic lecithotrophs (Table 1). This is surprising because, whereas pelagic lecithotrophic larvae are independent of the parent throughout development and are incapable of utilizing

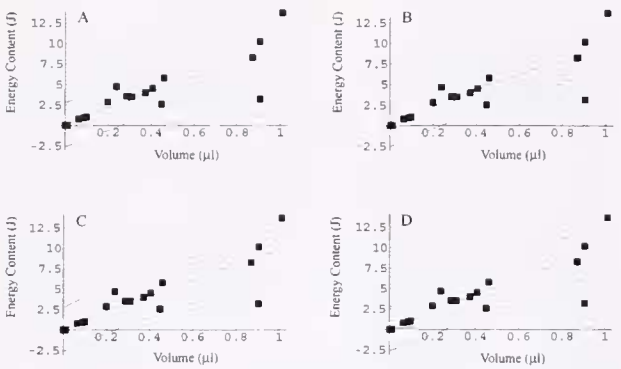

Figure 6. Plots of egg volume and energy content for the 38 species of echinoderms with planktotrophic or lecithotrophic development. Panels show different regression models fit to the data and the 95% confidence belts around the regression line. A, linear regression; B, power function; C, full allometric model; D, polynomial model.

planktonic food particles, brooders retain the offspring on or in the body of the parent and therefore have the potential to provide nutrition to the developing young.

Scaling relationships among free-spawners

Among free-spawning species, linear regression explains 84% of the variance in egg energy content in this sample of 38 species (Fig. 6). The best-fit linear regression passes through the origin (the intercept confidence interval includes zero) and has a slope of 9.87 (Table 5). The power function and the allometric models each explain 88% of the variance. Their slopes (9.64) are not different from the slope of the linear regression, and their scaling exponents (0.87) are not significantly different from 1. This indicates that energy content increases roughly in proportion to egg volume.

The predictive power of these scaling relationships does not improve substantially by restricting the analysis to development modes without offspring retention. Eggs that differ by 0.56–0.62 µl in volume have different predicted energy contents. Note that this is still more than half of the entire range of egg sizes in these two modes of development. How good is this? Volume is the most useful measure of egg size for comparison with content, but it is not easy to visualize. Biologists routinely report egg size as diameter because it is easy to measure and it is what one sees in an optical section under the microscope. Obviously, the diameter difference required to generate a difference of 0.56 µl in volume will depend on the size range of eggs considered. To illustrate the point, consider an egg with a diameter of 1000 µm; it has a volume of 0.52 µl. Eggs must be larger than 1250 µm in diameter in order to yield different predictions of content. However the egg of 1000 µm has a predicted content that is indistinguishable from the contents of all eggs that are smaller. In effect, all that can be concluded from the regression of size and content is that most lecithotrophs produce eggs with more energy in them than do planktotrophs.

Scaling relationships among species with nonfeeding development

The pelagic lecithotrophs and brooders together comprise the species with nonfeeding modes of development. Among these 24 species, all four regression models yield excellent fit, narrow parameter confidence intervals, and reasonably good predictive power (Fig. 7, Table 6). All of the models account for more than 99% of the variance in energy content. Both the power function (1.07) and allometric (1.08) model exponents are only slightly different from 1, indicating nearly proportional scaling of content with volume. The predictive power is good in that the minimum difference in egg volume needed for significantly different predictions of content is only 1.0 µl, 9% of the egg volume range in this sample. But as can be seen from the plot (Fig. 7), this difference allows predictions only between the lecithotrophs

Table 5

Regression parameters for the 38 species of echinoderms with planktotrophic or lecithotrophic development

Model	*a*	*b*	*c*	*k*	Fit	ΔX predict Y
Linear	0.099	9.870	—	—	0.839	0.56 µl
	[−0.400–0.599]	[8.407–11.333]				[55%]
Power	—	9.636	—	0.871	0.882	—
		[8.167–11.105]		[0.610–1.132]		
Allometric	−0.012	9.644	—	0.868	0.882	0.62 µl
	[−0.592–0.567]	[8.097–11.190]		[0.569–1.167]		[61%]
Polynomial	0.066	10.688	−0.957	—	0.880	—
	[−0.476–0.609]	[5.620–15.756]	[−6.627–4.712]			

Regression parameters are illustrated for each model in Table 2. Fit is the proportion of the total variance in egg energy content that is explained by the regression against egg volume. ΔX predict Y gives the minimum difference in egg volume needed to yield significantly different predictions of egg energy content.

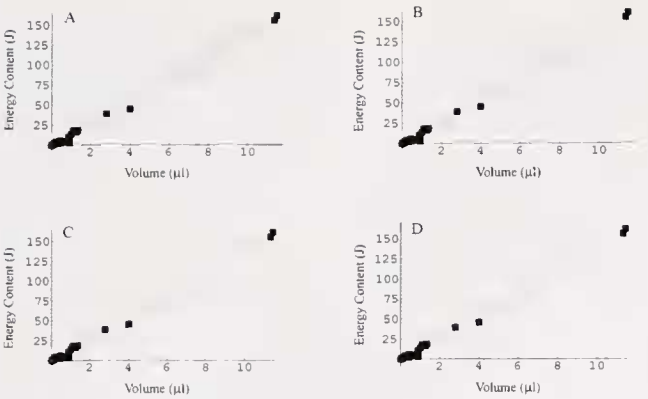

Figure 7. Plots of egg volume and energy content for the 24 species of echinoderms with lecithotropic or brooded development, excluding *Notasterias armata*. Panels show different regression models fit to the data and the 95% confidence belts around the regression line. A, linear regression; B, power function; C, full allometric model; D, polynomial model.

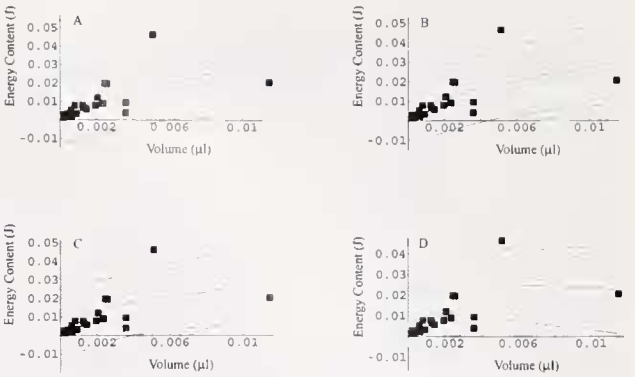

Figure 8. Plots of egg volume and energy content for the 22 species of echinoderms with feeding larvae, including *Clypeaster roseaceus*. Panels show different regression models fit to the data and the 95% confidence belts around the regression line. A, linear regression; B, power function; C, full allometric model; D, polynomial model.

as a group and between the four brooders with the largest eggs.

Scaling relationships for species with planktotrophic larval development

Planktotrophic species produce small eggs that develop into feeding larvae. The echinoid *Clypeaster rosaecus* has, for all previous analyses, been considered to be lecithotrophic because the energy content of the egg is sufficient to support complete larval development to metamorphosis (Emlet, 1986). However, since it has feeding larvae, it could be considered a facultative planktotroph. We analyzed the scaling relationships among planktotrophs with *C. rosaceus* included and excluded from the data. When *Clypeaster* is included there are 22 species with feeding larvae (Table 1). The linear regression model yields a relatively poor fit to the data, explaining only 37% of the variance in content (Fig. 8, Table 7). The power function and the allometric models explain 70%–72% of the variance, and the polynomial regression generates the best fit (77%). For all of these models the parameter confidence intervals are very broad, and none of the models have any predictive power (Table 7). Even the extremes in the range of egg sizes do not yield significantly different predictions of content. Excluding *Clypeaster* improves the fit of the regressions, but the parameter confidence intervals remain very large. Based on Hat Diagonals and residuals, we removed three additional species (*Encope aberrans, Encope michelini, Parastichopus californicus*) and then two more species from the planktotrophic dataset (*Luidia clathrata, Odontaster validus*). These changes did not result in better estimates of the regression parameters (CIs). Furthermore, the nonlinear models were drastically different for each subset of the data. The allometric model exponent varied from 0.335 (negative allometry) to 1.97 (positive allometry) as species were included or excluded from the analysis. However, the allometric exponent was not significantly different from isometric (1.0) for any of the

Table 6

Regression parameters for the 24 species of echinoderms with lecithotrophic or brooded development, excluding Notasterias armata

Model	*a*	*b*	*c*	*k*	Fit	ΔX predict Y
Linear	−1.318	13.848	—	—	0.995	1.00 µl
	[−2.735–0.098]	[13.435–14.261]				[9%]
Power	—	11.582	—	1.073	0.997	—
		[10.180–12.985]		[1.021–1.124]		
Allometric	0.326	11.279	—	1.083	0.997	1.03 µl
	[−1.614–2.265]	[8.998–13.560]		[1.002–1.164]		[9%]
Polynomial	−0.088	11.759	0.183	—	0.997	—
	[−1.745–1.568]	[9.951–13.568]	[0.028–0.339]			

Regression parameters are illustrated for each model in Table 2. Fit is the proportion of the total variance in egg energy content that is explained by the regression against egg volume. ΔX predict Y gives the minimum difference in egg volume needed to yield significantly different predictions of egg energy content.

Table 7

Regression parameters for the 22 species of echinoderms with feeding larvae, including Clypeaster roseaceus

Model	a	b	c	k	Fit	ΔX predict Y
Linear	0.004 [0.000–0.009]	2.482 [0.960–4.004]	—	—	0.367	— [>100%]
Power	—	0.403 [−0.340–1.145]	—	0.583 [0.256–0.910]	0.703	—
Allometric	−0.013 [−0.079–0.052]	0.151 [−0.200–0.502]	—	0.289 [−0.510–1.089]	0.717	— [>100%]
Polynomial	−0.001 [−0.007–0.004]	7.600 [3.719–11.480]	−481.456 [−825.424–−137.488]	—	0.765	—

Regression parameters are illustrated for each model in Table 2. Fit is the proportion of the total variance in egg energy content that is explained by the regression against egg volume. ΔX predict Y gives the minimum difference in egg volume needed to yield significantly different predictions of egg energy content.

subsets of planktotrophic species that we analyzed. Likewise, the coefficient of the second-order term of the polynomial regression varied from positive (upward curvature) to negative (downward curvature), but the 95% confidence interval for that parameter ranged from positive to negative for most analyses. The behavior of these models indicates that there is not a clear scaling trend among species with feeding larvae. This is consistent with the growing appreciation that planktotrophic species utilize a wide range of nutritional strategies and are characterized by different life history trade-offs across those strategies (Herrera *et al.*, 1996; McEdward and Janies, 1997; McEdward, 1997). At this point, with existing data, it is not possible to characterize the scaling relationships between egg size and energy content, and it is certainly impossible to use regression analysis to predict energy content from measurements of egg volume. Data on additional planktotrophic species might provide a clear picture of how egg energy scales with volume. However, it is also possible that energetic diversity among planktotrophs is considerable and clear trends for the entire suite of species with feeding larvae do not exist.

Scaling relationships among species with pelagic lecithotrophic development

There are data for 17 species (*Clypeaster* included) of echinoderms that have pelagic lecithotrophic development (Table 1). Egg volumes range from 0.007 to 1.01 μl, and energy contents range between 0.021 and 13.7 J · egg^{-1} (Fig. 9). The linear model explains 73% of the variance in egg energy content and the nonlinear models explain 88% (Table 8). The scaling exponents are 0.87 and 0.90 respectively for the power and allometric models, suggesting negative allometry, but neither is statistically different from isometry. The predictive power of all of the models is low, requiring differences in egg size on the order of the entire observed range of sizes (Table 8).

Scaling relationships among brooders

The eggs of nearly all brooders are larger and contain more energy than the eggs of pelagic lecithotrophs (Table 1). The only exception to this generalization is the brooding holothuroid *Cucumaria curata*, which has small eggs (0.52 μl, 4.58 J, Table 1). This is surprising because brooders have the potential to provide nutrition to the developing young (*e.g.*, Sewell and Chia, 1994; Byrne, 1996), whereas pelagic nonfeeding larvae are independent of the parent throughout development and are incapable of utilizing planktonic food particles. Is this a general result? Emlet *et al.* (1987) reported egg sizes, but not energy content, for nearly 200 species of asteroids and echinoids. They found that there was very little, if any, overlap in the egg size ranges of planktotrophs and lecithotrophs, but there was considerable overlap in the egg sizes produced by pelagic lecithotrophs and brooders (Emlet *et al.*, 1987, p. 108). In spite of the overlap, the largest eggs produced by both asteroids and echinoids occurred in brooding species. These observations

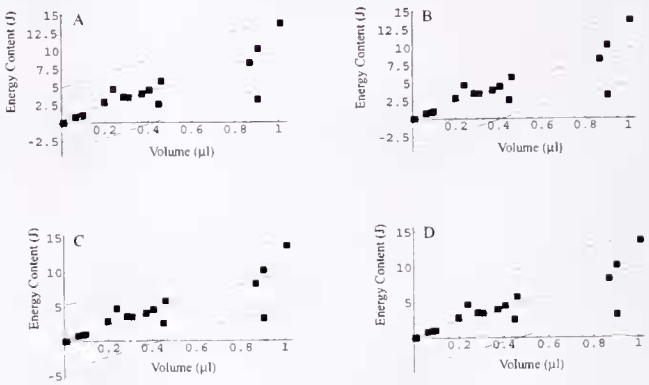

Figure 9. Plots of egg volume and energy content for the 17 species of echinoderms with lecithotrophic development, including *Clypeaster roseaceus*. Panels show different regression models fit to the data and the 95% confidence belts around the regression line. A, linear regression; B, power function; C, full allometric model; D, polynomial model.

Table 8

Regression parameters for the 17 species of echinoderms with lecithotrophic development, including Clypeaster roseaceus

Model	*a*	*b*	*c*	*k*	Fit	ΔX predict *Y*
Linear	0.421	9.385	—	—	0.727	0.97 μl
	[−1.196–2.038]	[6.217–12.554]				[97%]
Power	—	9.631	—	0.869	0.882	—
		[7.237–12.025]		[0.443–1.296]		
Allometric	0.137	9.524	—	0.900	0.882	—
	[−2.937–3.212]	[9.580–13.091]		[0.087–1.714]		[>100%]
Polynomial	0.510	8.722	0.659	—	0.882	—
	[−1.857–2.877]	[−4.122–21.567]	[−11.680–12.998]			

Regression parameters are illustrated for each model in Table 2. Fit is the proportion of the total variance in egg energy content that is explained by the regression against egg volume. ΔX predict *Y* gives the minimum difference in egg volume needed to yield significantly different predictions of egg energy content.

suggest that brooding, with its potential for post-spawning parental investment, does not necessarily result in lower levels of parental investment by means of the egg. Rather, it seems to provide the opportunity to increase levels of parental investment per offspring over those found in pelagic lecithotrophs. Possibly the functional requirements of pelagic life (*e.g.*, buoyancy control, swimming, settlement) preclude very large eggs and offspring. Alternatively, parental protection of brooded young could reduce the risk of offspring mortality sufficiently to allow allocation of more resources to individual young.

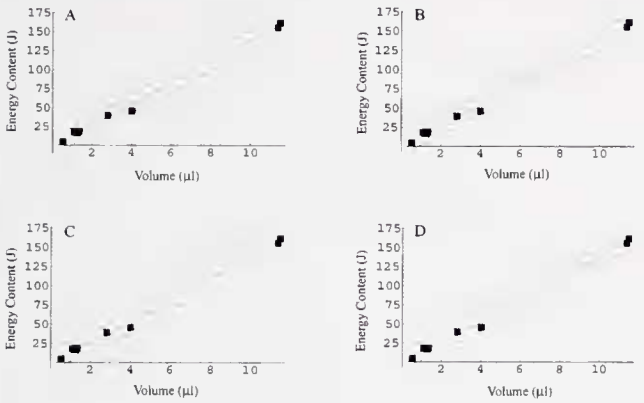

Figure 10. Plots of egg volume and energy content for the 8 species of echinoderms with brooded development, excluding *Notasterias armata*. Panels show different regression models fit to the data and the 95% confidence belts around the regression line. A, linear regression; B, power function; C, full allometric model; D, polynomial model.

The eight species of brooders (*Notasterias* excluded) are fit well by both the linear and nonlinear models (Fig. 10, Table 9). More than 99% of the variance in content is explained by each regression model. However, parameter confidence intervals are still quite wide; for example, the scaling exponent of the allometric model (1.15) is not significantly different from 1. The predictive power is reasonably good for both models, requiring egg size differences of 16%–17% of the observed range.

Discussion

Among echinoderms, larger eggs do contain more energy. The general pattern that is suggested by this study is

Table 9

Regression parameters for the 8 species of echinoderms with brooded development, without Notasterias armata

Model	*a*	*b*	*c*	*k*	Fit	ΔX predict *Y*
Linear	−1.495	13.897	—	—	0.996	1.74 μl
	[−6.788–3.798]	[13.018–14.775]				[16%]
Power	—	12.152	—	1.053	0.998	—
		[9.111–15.192]		[0.946–1.159]		
Allometric	4.414	9.277	—	1.153	0.998	1.86 μl
	[−6.389–15.218]	[2.102–16.453]		[0.858–1.447]		[17%]
Polynomial	3.056	10.566	0.264	—	0.999	—
	[−5.483–11.595]	[5.376–15.757]	[−0.142–0.669]			

Regression parameters are illustrated for each model in Table 2. Fit is the proportion of the total variance in egg energy content that is explained by the regression against egg volume. ΔX predict *Y* gives the minimum difference in egg volume needed to yield significantly different predictions of egg energy content.

that egg energy scales very nearly in direct proportion to egg volume across a remarkable range of egg sizes both within and among different modes of development. This seems to be a robust result that emerges from different analyses using different regression models and different methods and assumptions for calculating egg energy (see Jaeckle, 1995).

Statistically significant linear and nonlinear regressions were obtained in nearly all of these interspecific analyses. This demonstrates that some, and often a large proportion, of the variance in content is related to egg size. However, in many cases there were wide confidence intervals around the estimated regression parameters, suggesting caution in interpretation of the parameters. Whether the precision of regression parameter estimates will improve with new data for additional species or whether new data will confirm an underlying diversity in the egg size-content relationship is not clear. We believe that the latter possibility is likely, especially for moderate increases in the number of species analyzed. Once a substantial number of new species are added to the dataset and the underlying diversity is adequately sampled, then additional data should lead to more precise estimates of scaling patterns.

A statistically significant regression provides a means to predict content from a measurement of size. But a significant regression, even with a very good fit (% variance explained), does not ensure that predictions based on it will be useful or reliable. Although we have tried to bias the outcome by excluding some species or restricting the analysis to subsets of the data, in all of the cases examined here the predictive power of the regressions was poor. We strongly advocate explicit tests of regression results, whether the regression is used to describe scaling patterns or to make predictions from future measurements. At a minimum, we advocate evaluation of parameter confidence intervals and some test of the predictive power of the regression.

The analyses presented here clearly show how poor the predictive power of regressions can be, even when there is a good fit to the data. In some cases, the predictive power is poor because many of the data points are clustered at the low end of the egg size range. So that even if the minimum difference in egg size needed to yield significant predictions of content is a small percentage of the egg size range, the difference is quite large relative to the egg size differences among many of the species (*e.g.*, nonfeeding development, Fig. 7, Table 6). In other cases, the predictive power is low because the regression slope is shallow relative to the width of the confidence bands and the range of egg sizes (*e.g.*, lecithotrophs, Fig. 9, Table 8). In still other cases, the poor predictive power is the result of a poor fit between the regression and the data (*e.g.*, linear model for planktotrophs, Fig. 8A, Table 7) or a strongly curvilinear regression (*e.g.*, allometric model for planktotrophs, Fig. 8C, Table 7).

On the basis of our results in this study, we advocate use of the full allometric model for studies of scaling relationships. This model has the advantage of being simple and general (see also Emlet, 1989; Albrecht *et al.*, 1993; Ebert and Russell, 1994). It can capture linear and nonlinear patterns, can handle nonzero intercepts, and is reasonably easy to interpret. The most obvious disadvantages do not present serious problems. First, the allometric model cannot be converted to linear form (for ease of calculation) using logarithms, but log transformations are objectionable because they can strongly influence the fitting of model to data and the estimation of the regression parameters. Use of the allometric model requires nonlinear fitting algorithms, which are now available in many statistical and mathematical programs. Alternatively, effective iterative fitting methods can be easily programmed (see Manaster and Manaster, 1975; Albrecht *et al.*, 1993, or contact the authors for documented source code). The second disadvantage is that the allometric model cannot capture complex nonlinear patterns. There are relatively few cases in which scaling patterns have been convincingly shown to be complex. Furthermore, the parameters of complex regression models are often difficult to interpret biologically, in spite of providing very good fit to the data. The alternatives to the allometric model that we analyzed in this study all suffer from serious drawbacks. The linear model is too limited, since it cannot capture nonproportional (allometric) scaling, which is a common pattern in biology. The power function is simply a limited version of the allometric model that forces the regression to pass through the origin, an unnecessary and often erroneous assumption in biology, which also precludes evaluating the predictive power of the regression. The polynomial regression sometimes yielded a slightly better fit to the data, but there was no case in which the data were characterized by nonlinearity that could be fit with the polynomial but not the allometric model. Polynomial models, even low-order models such as the quadratic that we used in this study, are hard to interpret biologically.

One asteroid species, *Notasterias armata* (a brooder), is strikingly different in egg size or energy content relative to all other species. It potentially exerts extraordinary influence on the regression analyses. Given that these data are not the result of serious measurement error, it become an interesting problem to explain the basis for such different levels of egg provisioning in this Antarctic species. It has exceptionally large eggs (23.2 μl^{-1}), but the energy content is the same as that of *Diplasterias meridionalis* and *Diplasterias brucei* (Table 1). These two species are also Antarctic asteroids that brood their young. Their eggs are 3 times greater in volume than those of any other species in our data set, but their eggs are only half the size of *Notasterias* eggs. It is not obvious what selection pressures would favor substantially increased egg volume without increased egg

energy content, especially in an organism that broods its offspring.

Our conclusion from this study is that egg size is of limited value for fine-scale quantitative predictions of egg energy content and should be used with caution. This conclusion challenges a fundamental assumption in reproductive ecology and, as a result, increases the difficulty of understanding life-history patterns in marine invertebrates.

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